



Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv



Stream invertebrate communities are primarily shaped by hydrological factors and ultimately fine-tuned by local habitat conditions

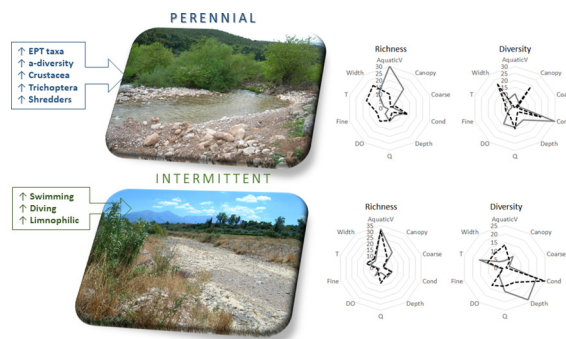
Ioannis Karaouzas^{*}, Christos Theodoropoulos, Aikaterini Vourka, Konstantinos Gritzalis, Nikolaos Th. Skoulidakis

Hellenic Centre for Marine Research, Institute of Marine Biological Resources and Inland Waters, 46.7 km Athens-Sounio Ave., 19013 Anavyssos, Greece

HIGHLIGHTS

- We explored how stream communities respond to their intra-annually changing natural environment.
- Perennial-intermittent sites were compared to identify habitat-selection mechanisms.
- Species richness and diversity are higher in perennial than intermittent rivers.
- Macroinvertebrates are primarily determined by hydrological-hydraulic variation.
- Upon hydrological stability, local environmental factors interact to define optimal habitats.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 25 November 2018
Received in revised form 7 February 2019
Accepted 8 February 2019
Available online 10 February 2019

Editor: Sergi Sabater

Keywords:

Species richness
Diversity
Species traits
Spatial
Temporal factors

ABSTRACT

The environmental factors that determine species richness and community structure in running waters have long been studied, but how these factors hierarchically and/or interactively influence benthic communities remains unclear. To address this research gap, we identified the principal abiotic factors that determine the taxonomic composition and functionality of stream macroinvertebrate communities and explored possible hierarchical and/or interactive patterns. We analyzed a large dataset from Greek rivers, and compared multiple macroinvertebrate metrics and traits between perennial and intermittent watercourses during wet and dry periods. We found that macroinvertebrates were primarily influenced by two ecological gradients: (i) aquatic vegetation-conductivity; and (ii) water temperature-canopy cover. Macroinvertebrates in perennial rivers were mainly influenced by the first gradient, whereas in intermittent rivers both gradients were important. Taxonomic richness and diversity were higher and temporally stable within years in perennial rivers, whereas in intermittent rivers, these metrics peaked during early summer, before the onset of streambed desiccation. The two environmental gradients determined the taxonomic richness and diversity in both spring and summer; however, a clear influence of hydrological factors (wetted width, water depth, flow velocity and discharge) was observed only in the intermittent samples. We conclude that the benthic invertebrate taxonomic richness and diversity in highly variable environments is primarily determined by hydrological variation and ultimately fine-tuned by local habitat factors. As climate change scenarios predict severe modification of hydrological and local habitat factors, this study concludes that in river management, hydrological restoration should be prioritized over other local habitat factors by maintaining natural hydrological variability, to ensure aquatic community richness and diversity.

© 2019 Elsevier B.V. All rights reserved.

^{*} Corresponding author.

E-mail address: ikarz@hcmr.gr (I. Karaouzas).

1. Introduction

Spatial and temporal environmental heterogeneity in freshwater ecosystems is determined by numerous scale-dependent factors which interact to influence the distribution of benthic organisms (Heino et al., 2003; Bonada et al., 2007; García-Roger et al., 2013). In Mediterranean-climate regions, seasonal variation in temperature and rainfall are primary evolutionary pressures that determine the structural and functional composition of instream communities (Gasith and Resh, 1999; Bonada et al., 2007; Cid et al., 2017). In these regions, three broad river flow-regime categories can be distinguished (Skoulikidis et al., 2017): perennial (flowing throughout the year), intermittent (with seasonal desiccation) and ephemeral (flowing only in response to precipitation or snowmelt events). Hydrological variability in Mediterranean river ecosystems is often extreme and strongly influences the benthic communities (Leigh and Datry, 2017; Theodoropoulos et al., 2018). Overall, the biological temporal heterogeneity of fluvial ecosystems has been found to decrease along with increasing flow permanence due to increasing flow stability (Bêche et al., 2006; Bonada et al., 2007). In contrast, spatial heterogeneity along this gradient may increase with increasing water permanence, if higher water levels and the increased land coverage create structurally diverse habitats (Bonada et al., 2007).

How local abiotic variables influence macroinvertebrate community variability has been explored in several studies (e.g. García-Roger et al., 2013; Datry et al., 2014). Substratum, water temperature and dissolved oxygen, and hydrological controls (including water depth, current velocity, wetted width, and discharge) are commonly considered as drivers of macroinvertebrate community composition (Poff, 1997; Richards et al., 1993; Leunda et al., 2009; Leigh, 2013). Much variation in instream communities reflects physical and chemical habitat changes resulting from intra- and interannual flow variation (Thompson and Townsend, 1999). Low flows reduce aquatic habitat availability, increase water temperature, conductivity and pH, and decrease dissolved oxygen concentrations, whereas high flows increase the hydrological effects on the stream bed, also causing changes in community structure (Hart and Finelli, 1999). Due to the extreme hydrological variation occurring as intermittent and ephemeral watercourses shift between wet and dry states, seasonal environmental factors are typically more variable in these systems than in perennial rivers (Bonada et al., 2006; García-Roger et al., 2011).

Thus, communities in these highly dynamic systems are very likely to experience frequent changes in their organization and assembly structure (Datry et al., 2014). However, ecologists are just starting to appreciate the temporal variation in macroinvertebrate community structure in these ecosystems (Datry et al., 2014; Datry et al., 2016; Tonkin et al., 2017). Understanding and predicting the dynamics of macroinvertebrate community structure will be necessary for the management, conservation and restoration of biodiversity in highly variable river ecosystems, which are being drastically altered by climate changes (van Vliet et al., 2013). Although the responses of benthic macroinvertebrates to the seasonally changing environment in perennial and intermittent rivers has received much attention (e.g. Bonada et al., 2007; Sánchez-Montoya et al., 2009; García-Roger et al., 2011; Santos and Stevenson, 2011), it still remains unclear which are the environmental factors that hierarchically determine macroinvertebrate assembly structure. Furthermore, if these hierarchical environmental factors remain the same across different river types (e.g. small mountainous rivers vs large floodplain rivers) is still a question of paramount importance for underpinning sustainable management of natural-water resources.

In this study, we explore the response of benthic macroinvertebrate communities in perennial and intermittent rivers to natural, intra-annual environmental variability. We explored macroinvertebrate responses to environmental variability, focusing on three specific questions: (i) Do abiotic factors have hierarchical and/or interactive

effects on the taxonomic and functional composition and diversity of benthic communities? (ii) Do abiotic factors and community responses to these factors differ between perennial and intermittent watercourses across different typological river systems? (iii) Can the relative contribution of the key environmental determinants of any spatial biological variation be quantified? To answer these questions, we analyzed a large benthic-invertebrate dataset from non-perturbed perennial and intermittent streams and rivers in Greece, and compared multiple benthic community metrics and traits between perennial and intermittent watercourses in wet and dry periods.

2. Methods

2.1. Data preparation

Physicochemical, habitat and biological data were assembled from the records of the Greek Surface Water Monitoring Programme (GSWMP) first management cycle (2012–2015), covering 449 sampling sites in Greece. Within the GSWMP, physicochemical, habitat and biological data were measured synchronously during spring and summer. Physicochemical data (pH, dissolved oxygen, water temperature and electrical conductivity) were recorded at each site using a portable multiparameter water monitoring probe (Aquaread AP2000). Wetted depth, width and water discharge were measured and the percentage of aquatic vegetation and the canopy cover were visually estimated. Substrate was visually categorized into two size classes, coarse (diameter > 4 mm) and fine (diameter ≤ 4 mm). Benthic macroinvertebrate samples were collected using a semi-quantitative 3-min kick-and-sweep method with a 25 cm × 25 cm hand net (500-μm mesh; Armitage and Hogger, 1994) with an additional 1-min sampling of marginal vegetation when present (Wright, 2000). Macroinvertebrate sampling in intermittent rivers during summer months was conducted only on sites where there was continuous flow and was not restricted to any available habitats, such as connected and disconnected pools. Samples were preserved in 70% ethanol, transferred to the laboratory and identified to family level. All samples were classified in a five-class system (bad, poor, moderate, good and high), based on the Hellenic Evaluation System 2 (HESY-2; Lazaridou et al., 2018) which fulfills the requirements of the European Union's Water Framework Directive 2000/60/EC (European Commission, 2000). To avoid bias, only samples classified as good or high ecological status were included in our analysis, comprising 497 samples from 229 sites across 76 river basins (Fig. 1); 435 samples were from perennial sites and 62 from intermittent sites (sampled before the annual dry phase).

2.2. Data analysis

2.2.1. Ordination of environmental-biological relationships

Canonical ordination techniques were used to examine relationships between environmental variables and macroinvertebrate families using the CANOCO 4.5 software. Eleven environmental variables were examined: (i) water temperature, (ii) % coarse sediment, (iii) % fine sediment, (iv) % aquatic vegetation, (v) % overhead canopy, (vi) water width, (vii) water depth, (viii) average flow velocity, (ix) discharge, (x) electrical conductivity, and (xi) dissolved oxygen saturation. We used detrended correspondence analysis (detrending by segments) to estimate the gradient length in standard deviation (SD) units and thus to select either canonical correspondence analysis (CCA) or redundancy analysis (RDA) (ter Braak, 1986). As the gradient length exceeded 2 SD, we applied a CCA (ter Braak, 1995).

To explore macroinvertebrate communities in relation to season and water permanence, samples were categorized into four groups: perennial spring, perennial summer, intermittent spring and intermittent summer. In addition, a typological-geomorphological grouping was applied using five groups according to the Mediterranean, WFD typology (RM-1: basin size 10–100 km², altitude between 200 and 800 m,

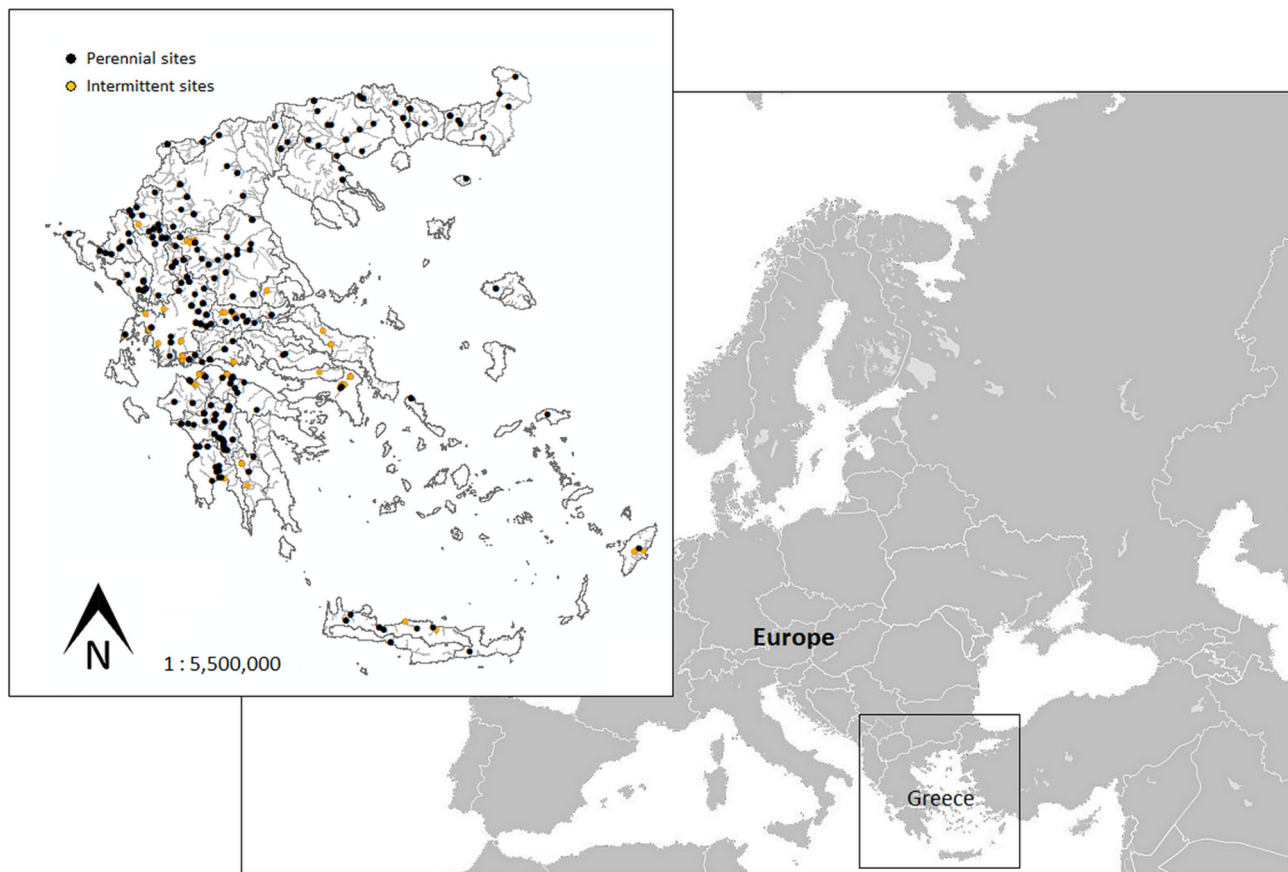


Fig. 1. Localities of the 229 sampling sites included in the analysis.

mixed geology; RM-2: 100–1000 km², <600 m, mixed geology; RM-3: 1000–10,000 km², altitude <600 m, mixed geology; RM-4: 10–1000 km², 400–1500 m, mixed geology; RM-5: 10–100 km², altitude <300 m, mixed geology – temporary; van de Bund, 2009) to examine biotic variation reflecting differences in altitude, geology and basin size. The most significant abiotic variables were selected with a Monte-Carlo permutation test, using 999 unrestricted permutations under a full model with automatic forward selection ($p < 0.05$). Macroinvertebrate abundance was square-root transformed prior to the CCA, to remove outliers and approximate normality. To identify the key-taxa contributing to seasonal differences shown by the CCA, an Indicator value analysis (IndVal; Dufrêne and Legendre, 1997) was applied using the 'multipatt' function of the 'indicpecies' package (De Cáceres and Legendre, 2009) in R version 3.5.1 (R Core Team, 2014).

2.2.2. Seasonal and hydrological groupings and comparisons

Benthic invertebrate trait metrics were calculated using the ASTERICS 3.1.1 software (<http://www.fliessgewaesser-bewertung.de/en/download/berechnung/>), which calculates ecological status based on the benthic invertebrate community, and includes a large number of metrics and other ecological information which can be used for data interpretation. A set of 26 metrics was selected to represent macroinvertebrate taxonomic composition and biological traits. These were taxon richness, diversity and abundance, EPT richness (number of families), functional feeding traits, current preferences and locomotion traits (Juhász, 2016). The following grouping schemes were applied to the dataset to explore seasonal and hydrological variation: (i) water permanence regime grouping (perennial samples - intermittent samples) - seasonal differences were separately explored for perennial and intermittent samples; (ii) seasonal grouping (spring samples - summer samples) - hydrological differences were separately explored

for each season; (iii) no grouping - (a) all seasons were pooled and perennial samples were compared with intermittent samples; (b) perennial and intermittent samples were pooled and spring samples were compared with summer samples. Because most macroinvertebrate metrics were not normally distributed, we applied the non-parametric, Kruskal-Wallis H test at $p < 0.05$, in the IBM SPSS 23.0 software package, to identify differences in macroinvertebrate metrics among the defined groups.

2.2.3. Influence of environmental variables within groups

Boosted regression tree (BRT) and generalized linear mixed-effects models (GLMM) were developed in R version 3.5.1 (R Core Team, 2014), to investigate the influence of environmental variables on selected macroinvertebrate metrics (richness, Shannon-Wiener diversity (H), Simpson's diversity index (D), %EPT, percentage of predators and percentage of shredders). For the BRT, we used the 'dismo package v1.0-15' (Hijmans et al., 2016). The models were developed with the bag fraction set to 0.5, the tree complexity set to 2 and the learning rate set between 0.0001 and 0.001 in order to achieve at least 1000 trees (Elith et al., 2008), and the relative contribution of each environmental factor (c) was calculated. GLMM were fitted using the 'gamlss' package (Stasinopoulos et al., 2017). We used the 'fittedrplus' (Delignette-Muller and Dutang, 2015) and 'logspline' (Kooperberg, 2018) packages to find the distribution that best fitted each biotic metric. The GLMM was then fitted using each environmental variable as a fixed factor. In the spring-summer comparisons, sampling year, water permanence regime (perennial-intermittent) and the river basin (76 basins) were used as random factors. In water permanence regime comparisons, sampling year, season (spring-summer) and river basin were used as random factors. Statistically significant correlations were identified at the $p < 0.05$, $p < 0.01$ and $p < 0.001$ levels and the

Table 1

Properties of the canonical correspondence analysis used to examine relationships between 11 environmental variables and 132 macroinvertebrate families.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.155	0.071	0.032	0.025	4.547
Species-environment correlations	0.714	0.656	0.557	0.498	
Cumulative percentage variance of species data	3.4	5.0	5.7	6.2	
Cumulative percentage variance of species-environment relation	44.0	64.1	73.2	80.4	
Sum of all eigenvalues					4.547
Sum of all canonical eigenvalues					0.352

Cox-Snell pseudo- R^2 (r) was additionally calculated using the 'rsq' package (Zhang, 2018).

3. Results

3.1. Canonical correspondence analysis

The first two CCA axes accounted for 22.5% of the variation in the macroinvertebrate data (Table 1). The first CCA axis accounted for 15.5% (44% of the explained variance), and was positively correlated with the % fine sediment (Fine), the % aquatic vegetation (AquaticV), electrical conductivity (Cond) and the % overhead canopy (Canopy) ($p = 0.002$; Fig. 2). The second CCA axis accounted for 7% (20% of

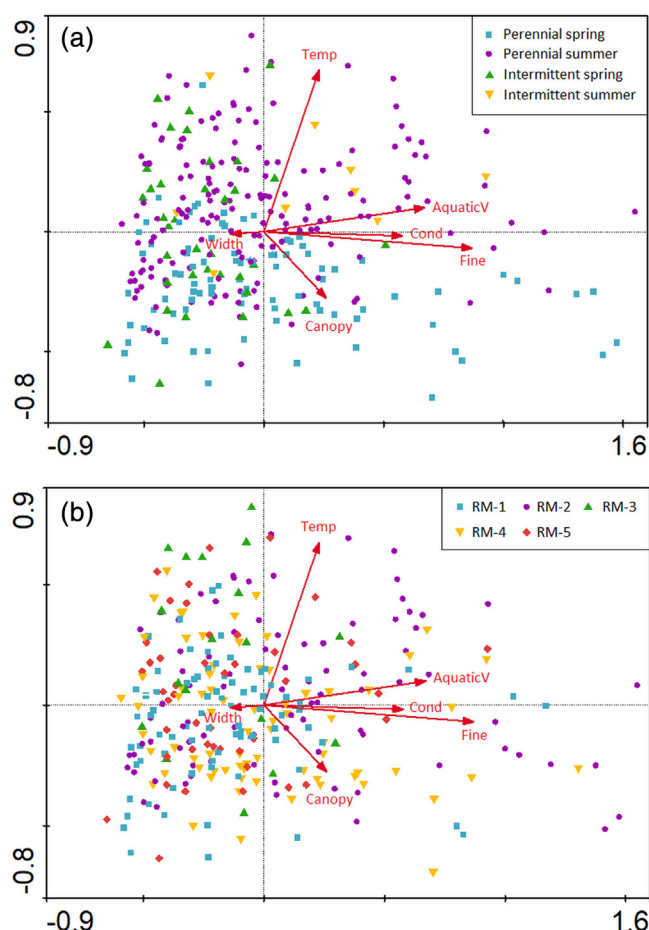


Fig. 2. Canonical correspondence analysis plot illustrating the relationship between the 132 macroinvertebrate taxa and the 11 environmental variables; (a) seasonal-hydrological grouping, (b) grouping based on river typology (van de Bund, 2009). Temp: water temperature; AquaticV: percentage of aquatic vegetation; Cond: electrical conductivity; Fine: percentage of fine sediment; Canopy: percentage of overhead canopy; Width: wetted width.

Table 2

Indicator value analysis (IndVal - Dufrêne and Legendre, 1997) results, showing the taxa that contributed to the seasonal variation observed within perennial samples in spring compared to summer.

Perennial sites	Indicator value	p value
Taxa - Spring		
Asellidae	0.406	0.006
Physidae	0.37	0.04
Erpobdellidae	0.344	0.014
Sphaeriidae	0.302	0.031
Lepidoptera	0.251	0.023
Taxa - Summer		
Euphaeidae	0.25	0.007

the explained variance), and was positively correlated with water temperature (Temp) and negatively correlated with the % overhead canopy (Canopy) ($p = 0.002$). The distribution of samples within the CCA ordination revealed strong seasonal differences in both perennial and intermittent samples. Perennial samples plotted along CCA axis 1, with perennial-spring samples concentrated in the negative part of the ordination, while most summer samples were concentrated in the positive part, partially overlapping in the mid-left part of the plot (Fig. 2a). The positioning of intermittent samples reflected a combination of two gradients (Temp-Canopy, AquaticV-Cond): intermittent-spring samples were concentrated at the left quadrants of the plot, while the intermittent-summer samples were concentrated at the upper-right quadrant (Fig. 2a). The first two CCA axes accounted for 25.1% of the explained variance at perennial sites and for >55% of the explained variance in the intermittent samples (data not shown). Considerable overlap among samples from different RM types (Fig. 2b) and between the perennial and intermittent samples suggests no comparable community composition across groups.

Table 3

Indicator-value analysis (IndVal - Dufrêne and Legendre, 1997), showing the taxa that contributed to the seasonal variation (spring-summer) observed within the intermittent samples.

Intermittent sites		
Taxa - Spring	Indicator Value	p value
Taeniopterygidae	0.535	
Corixidae	0.365	
Libellulidae	0.350	
Dugesidae	0.313	
Glossosomatidae	0.312	>0.05*
Curculionidae	0.286	
Hydrochidae	0.286	
Polycentropodidae	0.286	
Taxa - Summer		
Caenidae	0.849	0.008
Gomphidae	0.824	0.001
Hydroptilidae	0.808	0.002
Hydraenidae	0.799	0.002
Leuctridae	0.709	0.005
Dryopidae	0.674	0.001
Elmidae	0.672	0.035
Gammaridae	0.653	0.012
Leptoceridae	0.635	0.01
Tipulidae	0.59	0.027
Dixidae	0.555	0.015
Planorbidae	0.549	0.012
Gerridae	0.492	0.026
Hydrachnidia, Ancyliidae, Lymnaeidae, Psychodidae, Rhagionidae, Anthomyiidae, Lestidae, Lepidoptera, Psychomyiidae, Helophoridae, Erpobdellidae, Mesoveliidae, Mysidae, Polychaeta, Potamanthidae, Scatophagidae, Sciomyzidae, Lepidostomatidae, Bithyniidae, Glossiphoniidae	Ranged from 0.266 to 0.486	>0.05*

* IndVal associations were identified for these taxa but were not statistically significant.

3.2. Indicator value analysis

Based on the IndVal analysis, specific taxa contributed to the seasonal differences observed in the CCA for both perennial and intermittent communities (Tables 2 and 3). Asellidae, Physidae, Erpobdellidae, Sphaeriidae and Lepidoptera were associated with perennial samples in spring (IndVal: 0.25–0.406; $p < 0.05$), whereas summer-perennial samples were primarily differentiated by the higher abundances of Euphaeidae (IndVal: 0.25; $p < 0.05$) (Table 2). No significant associations were observed between taxa and intermittent samples in spring. In contrast, many taxa (e.g. Caenidae, Gomphidae, Hydroptilidae, Hydraenidae, Leuctridae, Dryopidae, Elmidae, Gammaridae, Leptoceridae, Tipulidae) were strongly associated with intermittent samples in summer (IndVal: 0.492–0.849; $p < 0.05$; Table 3).

3.3. Comparisons between seasons and water permanence groups

Richness and diversity differed between seasons in both perennial and intermittent samples (Kruskal-Wallis $p < 0.01$; Table 4). Both metrics were higher for perennial compared to intermittent communities, and in summer compared to spring ($p < 0.01$). Seasonal differences were evident both when perennial and intermittent sites pooled together and analyzed separately (Table 4).

Odonata, Trichoptera, Plecoptera, Heteroptera, Coleoptera and Diptera (i.e. most insect orders) were more abundant during summer in both the perennial ($p < 0.01$) and intermittent samples ($p < 0.05$). Shredders, predators and grazers-scrappers were more abundant during summer in both perennial ($p < 0.01$) and intermittent samples ($p < 0.05$). Rheophilic taxa were more abundant during spring ($p < 0.01$) and limnophilic taxa were more abundant during summer ($p < 0.01$).

Fewer differences were observed between the perennial and intermittent samples than between spring and summer samples. When spring and summer samples were pooled, richness, diversity

and % of EPT taxa were higher in perennial than intermittent samples ($p < 0.01$). Trichoptera and Coleoptera abundances were also higher ($p < 0.01$), whereas shredders and predators were more abundant in the perennial samples ($p < 0.01$). However, when spring and summer samples were analyzed separately, the differences in richness and diversity were observed only during spring. Other feeding types (gatherers-collectors, active and passive filter feeders) differed between the perennial and intermittent samples in summer ($p < 0.05$).

3.4. Relationships between environmental variables and biotic metrics

The AquaticV-Cond and Temp-Canopy gradients of the CCA were also observed in both the BRT and the GLMM models: aquatic vegetation, overhead canopy and conductivity were major determinants of taxonomic richness in both spring ($c = 58.4\%$, $r = 0.34$, $p < 0.05$) and summer ($c = 49.3\%$, $r = 0.21$, $p < 0.01$) (Fig. 3; Table A1). Temperature and discharge also had a strong contribution to taxonomic richness variation (spring: $c = 13.11\%$ and summer: 25.08%). The H index was influenced by both CCA gradients; specifically water depth ($c = 23.23\%$, $r = 0.67$, $p < 0.1$), conductivity ($c = 19.62\%$, $r = 0.54$, $p < 0.01$), temperature ($c = 15.88\%$, $r = 0.56$, $p < 0.01$) and discharge ($c = 13.73\%$, $r = 0.68$, $p < 0.1$) were the major determinants of diversity during spring, whereas aquatic vegetation ($c = 13.62\%$) and conductivity ($c = 24.82\%$) were major contributors during summer. Similarly, the AquaticV-Cond gradient contributed 37.19% and 34.67% to variation in the D index and %EPT, respectively ($r = 0.46$ – 0.48 , $p < 0.01$), during spring (but water depth and discharge also had a high contribution of 33.86% for the D index) and 36.96%–35.49% ($r = 0.038$ – 0.21 , $p < 0.01$) during summer. For predators, conductivity contributed 22.1%, dissolved oxygen 18.7% ($r = 0.28$, $p < 0.05$) and the % coarse substrate contributed 15.06% during spring, whereas discharge, depth, wetted width and water temperature were the major determinants during summer (overall $c = 82.59\%$). For shredders, temperature, dissolved

Table 4

Comparison of the selected metrics between seasons and water permanence groups (Per: Perennial, Int: Intermittent).

Groups	No grouping				Seasonal grouping				Hydrological grouping			
	Per		Int		Spring		Summer		Perennial		Intermittent	
	Spring	Summer	Spring	Summer	Per	Int	Per	Int	Spring	Summer	Spring	Summer
Metrics												
Abundance												
Richness	↑**	↓**	↓**	↑**	↑**	↓**			↓**	↑**	↓**	↑**
Shannon Diversity (H)	↑**	↓**	↓**	↑**	↑**	↓**			↓**	↑**	↓**	↑**
Simpson Diversity (D)	↑**	↓**	↓**	↑**	↑**	↓**			↓**	↑**	↓**	↑**
% Gastropoda			↓*	↑*			↑*	↓*			↓**	↑**
% Crustacea	↑*	↓*			↑**	↓**					↓**	↑**
% Odonata			↓**	↑**					↓**	↑**	↓**	↑**
% Trichoptera	↑**	↓**	↓**	↑**	↑*	↓*	↑*	↓*	↓**	↑**	↓*	↑*
% Plecoptera			↓**	↑**					↓**	↑**		
% Ephemeroptera												
% Heteroptera			↓**	↑**					↓**	↑**	↓*	↑*
% Coleoptera	↑**	↓**	↓**	↑**					↓**	↑**	↓**	↑**
% Diptera			↓**	↑**					↓**	↑**		
% Hydrachnidia	↑*	↓*	↓**	↑**					↓**	↑**	↓*	↑**
Shredders	↑**	↓**	↓**	↑**	↑*	↓*			↓**	↑**	↓**	↑**
Grazers-Scrapers			↓**	↑**			↑**	↓**	↓**	↑**		
Gatherers-Collectors							↑*	↓*	↑**			
Predators	↑**	↓**							↓**	↑**	↓*	↑*
Active Filter Feeders							↓*	↑*	↓**	↑**	↓*	↑*
Passive Filter Feeders							↓*	↑*				
Swimming-Diving	↓**	↑**	↑**	↓**			↓*	↑*	↑**	↓**		
Sprawling-Walking							↓*	↑*	↑**	↓**		
% EPT			↑*	↓*	↓**	↑**	↑*	↓*	↑**	↓**	↑*	↓*
EPT (number of families)	↑**	↓**			↑**	↓**	↑*	↓*			↑**	↓**
Type RP			↑**	↓**			↑**	↓**	↑**	↓**	↑**	↓**
Type LP			↓**	↑**			↓*	↑*	↓**	↑**	↓**	↑**

↑ Mean value of variable is higher in the specific group, ↓ Mean value of variable is lower in the specific group.

* $p < 0.05$.

** $p < 0.01$.

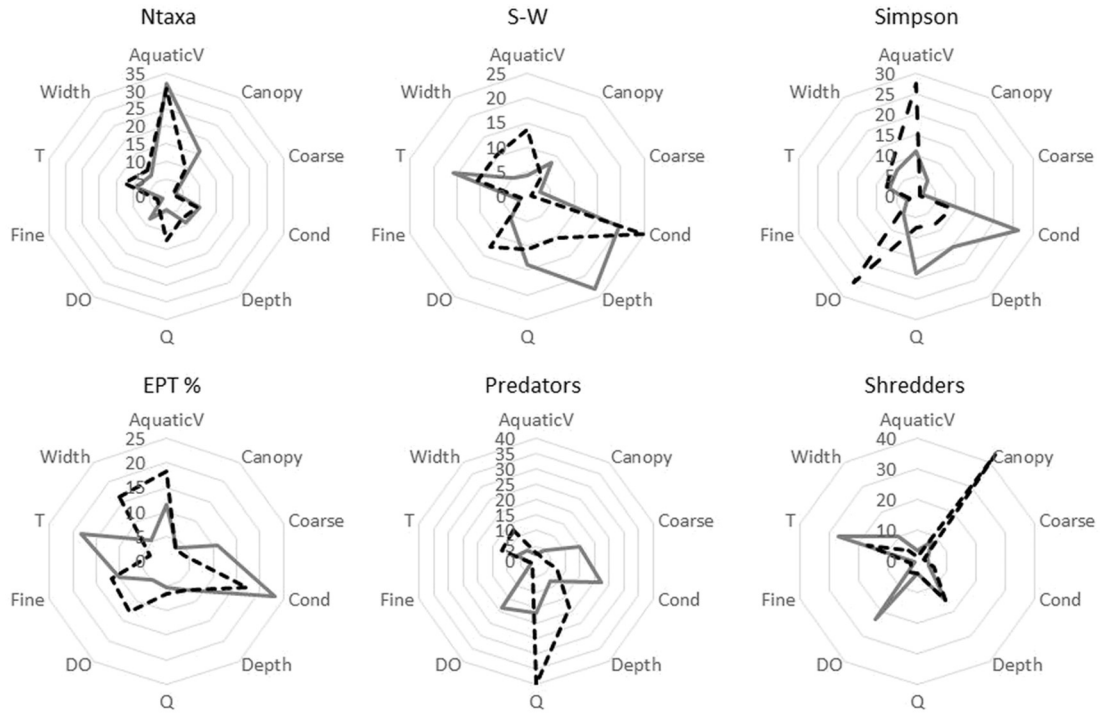


Fig. 3. Relative influence of selected environmental variables on the metrics and traits, which differed between spring and summer samples. Grey line: spring samples; black dashed line: summer samples.

oxygen, water depth and wetted width contributed 76.17% (BRT) during spring, while overhead canopy ($r = 0.13$, $p < 0.01$), temperature ($r = 0.06$, $p < 0.01$) and water depth ($r = 0.062$, $p < 0.05$) contributed 75.55% during summer.

The same gradients also determined differences between the perennial and intermittent samples (Fig. 4; Table A2). Taxonomic richness in the perennial samples was mostly influenced by aquatic vegetation ($c = 30\%$, $r = 0.28$, $p < 0.01$), wetted width ($c = 13\%$) and conductivity

($c = 11\%$). In intermittent samples, the same predictors showed a high overall contribution to taxonomic richness ($c = 44\%$). Diversity indices in perennial samples were influenced by aquatic vegetation, conductivity and dissolved oxygen ($c = 53.71\%$ and 73.14% , respectively, $r = 0.02$ – 0.04 , $p < 0.01$), whereas discharge and depth influenced the H index ($c = 23.64\%$). In intermittent samples, the overhead canopy, conductivity, discharge and wetted width were the major determinants (overall contribution 80.58% for H and 74.59% for D indices). The

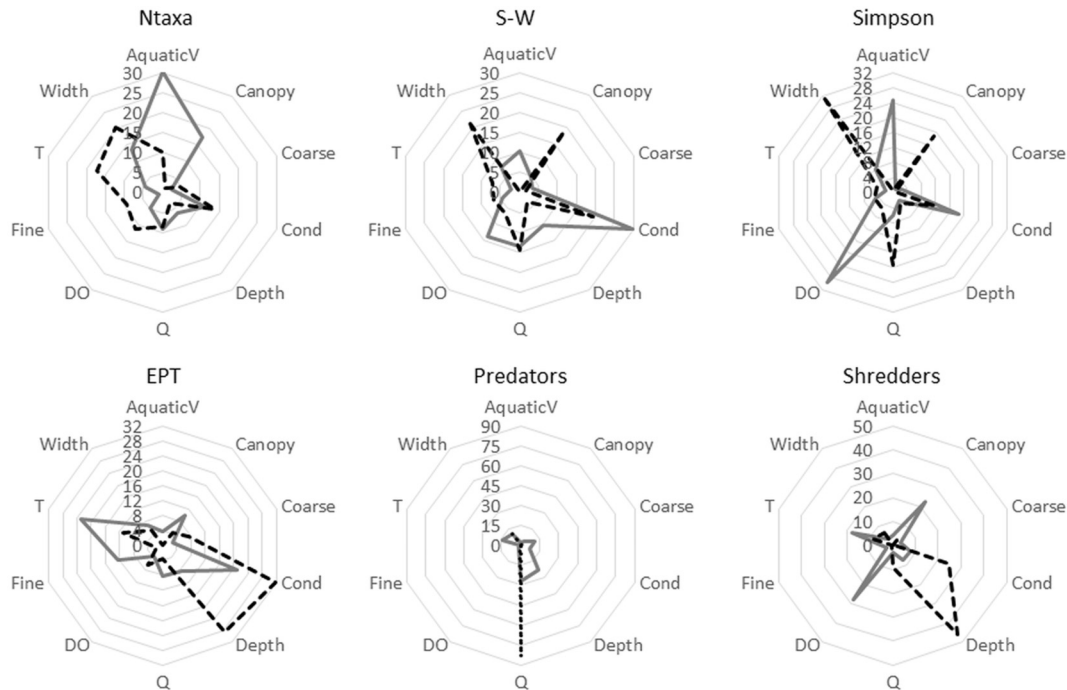


Fig. 4. Relative influence of selected environmental variables on the metrics and traits, which differed between perennial and intermittent samples. Grey line: perennial samples; black dashed line: intermittent samples.

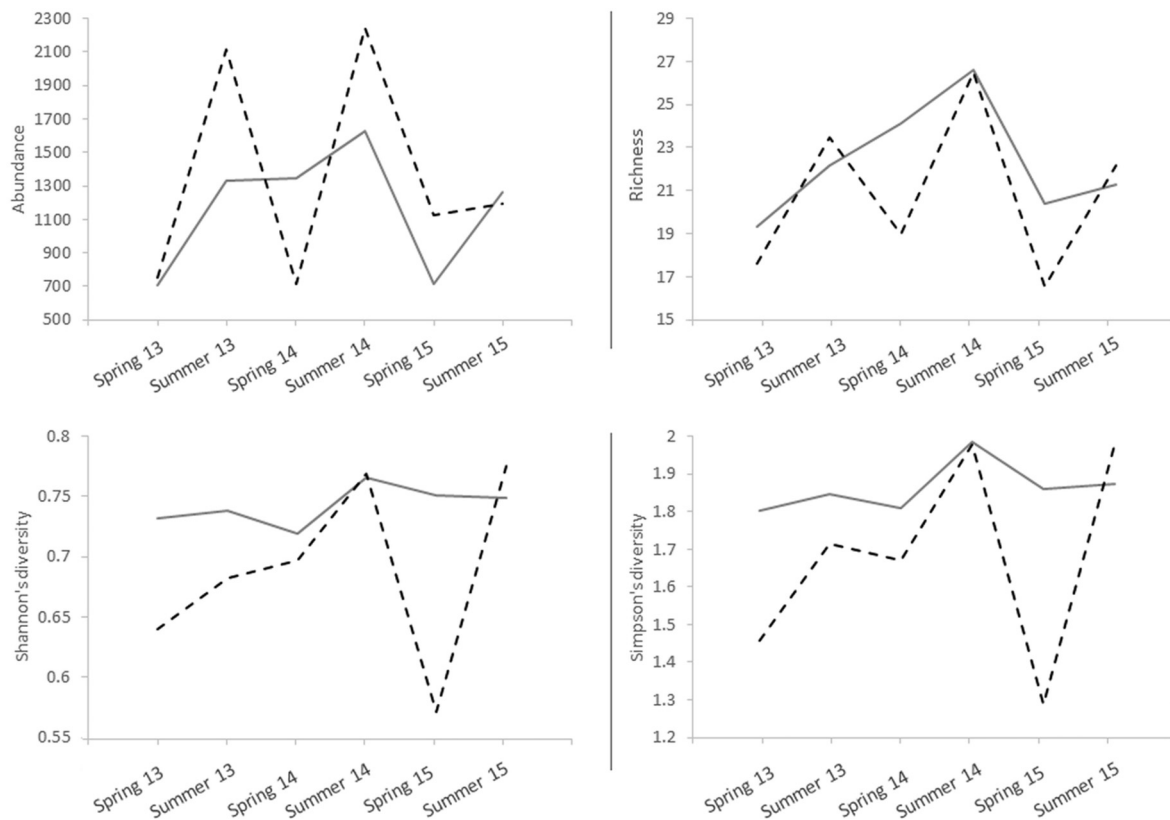


Fig. 5. Seasonal variation of the mean values of taxonomic metrics between perennial and intermittent samples. Grey line: perennial samples; black dashed line: intermittent samples.

abundance of EPT taxa in the perennial samples was influenced by temperature ($c = 22.88\%$, $r = 0.35$, $p < 0.01$), conductivity ($c = 21.04\%$, $r = 0.35$, $p < 0.05$), the percentage of fine substrate ($c = 12.48\%$, $r = 0.36$, $p < 0.01$) and the overhead canopy ($c = 10\%$). In the intermittent samples, conductivity, temperature and water depth were the major determinants of EPT taxa ($c = 71.4\%$, $r = 0.46$ – 0.73 , $p < 0.01$). Discharge was a major determinant of predator abundance in intermittent samples ($c = 83.64\%$, $r = 0.16$, $p < 0.05$ in intermittent samples). Shredders were mostly influenced by dissolved oxygen, overhead canopy and temperature in perennial samples (overall $c = 69.49\%$, $r = 0.08$ – 0.1 , $p < 0.01$), and by conductivity and depth in intermittent samples (overall 70.43% , $r = 0.46$ – 0.5 , $p < 0.05$). Based on the described differences, macroinvertebrate community metrics were more variable between seasons at intermittent compared to perennial sites (Fig. 5).

4. Discussion

4.1. Distribution of benthic macroinvertebrates in perennial and intermittent rivers

The findings of this study highlight a clear discrimination of the macroinvertebrate communities of perennial and intermittent sites, mostly attributed to the different variability in environmental factors. Overall, taxa richness was higher in perennial than intermittent rivers. The most notable differences between the intermittent and perennial communities were the higher total and EPT richness and the higher relative abundances of Trichoptera and Coleoptera in the perennial samples. Although some degree of seasonal variability between spring and summer samples was evident, our results agree with numerous previous studies (e.g. Eady et al., 2014; Giam et al., 2017; Stitz et al., 2017). Increased aquatic habitat connectivity that favors taxa dispersal (Ward et al., 1999), as well as higher habitat diversity and stability may contribute to higher richness in perennial streams (Bonada et al., 2007). In

addition, total richness declines when a reach dries due to desiccation sensitivity, although some taxa will first perish in pools due to oxygen depletion and extreme temperatures (Bêche et al., 2006). In agreement with Bonada et al. (2006), higher EPT richness was observed in perennial rivers during higher flow conditions (i.e. spring) and higher Odonata, Coleoptera and Hemiptera (OCH) taxa richness during summer months. As reported by Muñoz (2003), shredders were more abundant in perennial sites. In perennial streams, particulate organic matter is present all year thus favoring the growth of detritivorous groups. In contrast, intermittent rivers display seasonal fluctuations in the input of organic matter (higher in autumn and winter; low or no input during summer); hence higher biomasses of shredders and collectors are found mainly during autumn and winter. The distinct taxonomic assemblages found in intermittent and perennial sites can be attributed to adaptation to flow types (lentic-rheophilic) and to the available type of food resources (shredders in permanent flow conditions; predators in low flow conditions).

4.2. Factors affecting macroinvertebrate distribution in perennial and intermittent rivers

Aquatic vegetation, temperature, conductivity, fine sediment and canopy have previously been identified as the most important factors affecting macroinvertebrate community composition of intermittent sites during summer (Rocha et al., 2012). Drying events and low flow, which usually occur during summer, influence the local conditions including physical and chemical parameters, such as water temperature, conductivity and oxygen content (Stubington et al., 2009; Leigh, 2013), which causes changes in stream macroinvertebrate communities (Richards et al., 1993; Kalogianni et al., 2017; Karaouzas et al., 2018).

The critical influence of hydrological variability on the distribution of benthic macroinvertebrates was clearly indicated by both the BRT and the GLMM models. Although the seasonal comparison indicated that the

same factors (water temperature, dissolved oxygen, aquatic vegetation, conductivity and overhead canopy) influenced taxonomic richness and diversity in spring and summer (whereas no hydrological influence was evident), comparison of water permanence groups showed a clear influence of the wetted width, water depth and discharge on the richness and diversity of the intermittent samples. The role of hydrological variables as drivers of benthic macroinvertebrate distribution in hydrologically variable aquatic environments has been previously highlighted (Gore et al., 2001; Chessman, 2003; Wood and Armitage, 2004; Fonnesu et al., 2005).

Our results also showed a specific seasonal pattern of macroinvertebrate richness and diversity variation, which differed between perennial and intermittent rivers, similar to the findings of Giam et al. (2017); in perennial rivers, taxonomic richness, diversity, and to a lesser extent abundance, remained temporally stable between spring and summer, reflecting greater hydrological stability. In contrast, richness and diversity peaked during summer in intermittent rivers, just before the onset of streambed desiccation, reaching values similar to those of the perennial samples, but were significantly lower in spring, following the increased hydrological variability between sampling and the preceding summer (i.e. summer dry period; high, rainfall-induced flow variability during autumn and winter). Differences in taxonomic richness and diversity between perennial and intermittent rivers have been well-documented; however the results among studies are contrasting. Lower richness and diversity has often been reported during the dry season (Boulton and Lake, 1992; Bêche et al., 2006; Wooster and DeBano, 2018), but the opposite pattern was observed our study and has previously been reported (Giam et al., 2017; Stitz et al., 2017). Such increases in richness and diversity are mainly associated with flow permanence (Feminella, 1996; Stitz et al., 2017) or may reflect the concentration of organisms in a declining area of submerged habitat (Stubington et al., 2011). Such observations emphasize the timing of summer sampling relative to flow cessation or habitat contraction as a critical influence on diversity, richness and densities (Bogan et al., 2013; Wooster and DeBano, 2018).

When the critical influence of hydrological factors decreases due to hydrological stabilization after flow resumption, the distribution of benthic macroinvertebrates is differentiated ('fine-tuned') based on local habitat characteristics. In our study, these variables were the percentage of aquatic vegetation, conductivity, water temperature and percentage of overhead canopy. This was evidenced by considerable overlap between intermittent-spring and some of the intermittent-summer samples with the perennial-spring and perennial-summer samples on the CCA ordination; the latter were strongly influenced by the aquatic vegetation (+) conductivity (+) gradient and the temperature (+) overhead canopy (−) gradient. The environmental factors associated with both gradients have previously been considered as major drivers of the seasonal benthic-invertebrate variation (e.g. Friberg et al., 2001; Bonada et al., 2005; Miller et al., 2007; Leunda et al., 2009).

Other environmental variables may also be influential, including temperature, associated with dissolved oxygen and slope, which has been identified as the primary determinant of macroinvertebrate assemblages in some studies (Skoulikidis et al., 2009; Beltrán et al., 2011). Others have indicated a temperature-conductivity gradient (Friberg et al., 2001; Bonada et al., 2005; Miller et al., 2007), including aquatic vegetation (Leunda et al., 2009). Shading, strongly related to the overhead canopy, has also been reported as a significant driver of macroinvertebrate assemblages (Collier, 1995; Fuller et al., 2008).

4.3. Identifying hierarchical and interactive patterns of environmental-biotic relationships

An integrative interpretation of our results suggests that benthic invertebrate taxonomic richness and diversity in rivers with high hydrological variability is primarily determined by hydrological variation and is ultimately fine-tuned by the local environment. Specifically, the benthic fauna persisting in intermittent systems experiences

considerable hydrological variability and tolerates suboptimal conditions of specific abiotic factors, such as low oxygen concentrations and high water temperatures. This suggests a first-level, hierarchical prioritization of hydrology over other environmental influences on community composition. Upon flow resumption and stabilization, macroinvertebrates distribution becomes influenced by a second set of interacting habitat variables, including aquatic vegetation, conductivity, water temperature and overhead canopy.

In particular, the AquaticV-Cond and Temp-Canopy gradients were the main determinants of seasonal differences in the benthic invertebrate metrics. Their influence was stronger during stable flow conditions in perennial streams. In contrast, water depth, wetted width and water discharge had the highest influence in intermittent rivers during the summer. Thus, the highly variable macroinvertebrate community patterns observed for the intermittent samples were critically determined by the highly variable hydrological conditions between spring and summer, rather than by the AquaticV-Cond and Temp-Canopy gradients. In contrast, the relatively low hydrological variability at the perennial sites resulted in more stable community patterns, which were consequently determined and/or fine-tuned by the percentage of aquatic vegetation, water temperature, overhead canopy and conductivity.

5. Conclusions

Our results revealed that benthic macroinvertebrate richness and diversity are shaped primarily by hydrological variability and secondly by local habitat factors. The influence and hierarchy of both hydrological and local habitat factors did not vary across different stream typologies. Habitat availability changes seasonally through hydrologic variability which forces stream communities to be restructured again and again within a short period of time. Macroinvertebrates are regularly required to tolerate suboptimal environmental conditions which are expected to exacerbate due to climate change. Thus failing to recognize the fact that maintaining the spatial and temporal dynamics of stream ecosystems is essential, we may fail to inhibit biodiversity loss.

In a changing climate, the variable response of macroinvertebrates to the intra-annual environmental variation highlight the need for a multi-level approach to aquatic ecosystem management, in which hydrological restoration should be prioritized over other environmental factors. Protecting the natural flow variability in both perennial and intermittent rivers will ensure the presence of suitable habitats to support rich and diverse benthic communities, which may be further differentiated based on the interaction of local environmental factors.

Acknowledgements

The data of this study were collected during the Greek National Water Monitoring project, funded by the Hellenic Ministry of Environment and Energy (<http://www.ypeka.gr>). We thank the personnel of the Institute of Marine Biological Resources and Inland Waters involved in the Greek National Monitoring programme, who carried out or assisted in field and laboratory work. We are very grateful to Dr. Rachel Stubington for her valuable constructive comments and for English proof-reading of the manuscript. We would also like to thank Dr. Sergi Sabater and the three anonymous reviewers for their comments and suggestions towards the improvement of this manuscript.

The authors declare no conflict of interest.

CRedit author statement

Ioannis Karaouzas: Conceptualization, Investigation, Methodology, Writing – Original draft preparation; **Christos Theodoropoulos:** Formal Analysis, Investigation, Writing – Original draft preparation; **Aikaterini Vourka:** Formal Analysis, Investigation, Writing – review & editing; **Konstantinos Gritzalis:** Investigation, Writing – review & editing; **Nikolaos Skoulikidis:** Writing – review & editing, Project Administration.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.02.134>.

References

- Armitage, P.D., Hogger, J., 1994. Invertebrates' ecology and survey. In: Ward, D., Holmes, N., Jose, P. (Eds.), *The New Rivers and Wildlife Handbook*. Sandy RSPB, Bedfordshire, pp. 151–159.
- Bêche, L.A., McElravy, E.P., Resh, V.H., 2006. Long-term seasonal variation in the biological traits of benthic-macroinvertebrates in two Mediterranean climate streams in California, USA. *Freshw. Biol.* 51, 56–75. <https://doi.org/10.1111/j.1365-2427.2005.01473.x>.
- Beltrán, L., Miserendino, M.L., Pessacq, P., 2011. Life history, seasonal variation and production of *Andesiops torrens* (Lugo-Ortiz and McCafferty) and *Andesiops peruvianus* (Ulmer) (Ephemeroptera: Baetidae) in a headwater Patagonian stream. *Limnologia* 41, 57–62. <https://doi.org/10.1016/j.limno.2010.07.002>.
- Bogan, M.T., Boersma, K.S., Lytle, D.A., 2013. Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network. *Freshw. Biol.* 58, 1016–1028. <https://doi.org/10.1111/fwb.12105>.
- Bonada, N., Zamora-Muñoz, C., Rieradevall, M., Prat, N., 2005. Ecological and historical filters constraining spatial caddisfly distribution in Mediterranean rivers. *Freshw. Biol.* 50, 781–797. <https://doi.org/10.1111/j.1365-2427.2005.01357.x>.
- Bonada, N., Rieradevall, M., Prat, N., Resch, V.H., 2006. Benthic macroinvertebrate assemblages and macrohabitat connectivity in Mediterranean-climate streams of northern California. *J. N. Am. Benthol. Soc.* 25, 32–43. [https://doi.org/10.1899/0887-3593\(2006\)25\[32:BMAAMC\]2.0.CO;2](https://doi.org/10.1899/0887-3593(2006)25[32:BMAAMC]2.0.CO;2).
- Bonada, N., Rieradevall, M., Prat, N., 2007. Macroinvertebrate community structure and biological traits related to flow permanence in a Mediterranean river network. *Hydrobiologia* 589, 91–106. <https://doi.org/10.1007/s10750-007-0723-5>.
- Boulton, A.J., Lake, P.S., 1992. The ecology of two intermittent streams in Victoria, Australia. III. Temporal changes in faunal composition. *Freshw. Biol.* 27, 123–138. <https://doi.org/10.1111/j.1365-2427.1992.tb00528.x>.
- Chessman, B.C., 2003. New sensitivity grades for Australian river macroinvertebrates. *Mar. Freshw. Res.* 54, 95–103. <https://doi.org/10.1071/MF02114>.
- Cid, N., Bonada, N., Carlson, S.M., Grantham, T.E., Gasith, A., Resh, V.H., 2017. High variability is a defining component of Mediterranean-climate rivers and their biota. *Water* 9, 52. <https://doi.org/10.3390/w9010052>.
- Collier, K.J., 1995. Environmental factors affecting the taxonomic composition of aquatic macroinvertebrate communities in lowland waterways of Northland, New Zealand. *N. Z. J. Mar. Freshw. Res.* 29, 453–465. <https://doi.org/10.1080/00288330.1995.9516679>.
- Datry, T., Larned, S.T., Fritz, K.M., Bogan, M.T., Wood, P.J., Meyer, E.I., Santos, A.N., 2014. Broad-scale patterns of invertebrate richness and community composition in temporary rivers: effects of flow intermittence. *Ecography* 37 (1), 94–104.
- Datry, T., Bonada, N., Heino, J., 2016. Towards understanding the organisation of metacommunities in highly dynamic ecological systems. *Oikos* 125 (2), 149–159.
- De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90, 3566–3574.
- Delignette-Muller, M.L., Dutang, C., 2015. *fitdistrplus: an R package for fitting distributions*. *J. Stat. Softw.* 64 (4), 1–34.
- Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366.
- Eady, B.R., Hill, T.R., Rivers-Moore, N.A., 2014. Shifts in aquatic macroinvertebrate community structure in response to perennality, southern Cape, South Africa. *J. Freshw. Ecol.* 29, 475–490. <https://doi.org/10.1080/02705060.2014.910146>.
- Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. *J. Anim. Ecol.* 77, 802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>.
- European Commission, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for community action in the field of water policy. *Off. J. Eur. Communities* L327, 1–72.
- Feminella, J.W., 1996. Comparison of benthic macroinvertebrate assemblages in small streams along a gradient of flow permanence. *J. N. Am. Benthol. Soc.* 15, 651–669. <https://doi.org/10.2307/1467814>.
- Fonnesu, A., Sabetta, L., Basset, A., 2005. Factors affecting macroinvertebrate distribution in a Mediterranean intermittent stream. *J. Freshw. Ecol.* 20, 641–647. <https://doi.org/10.1080/02705060.2005.9664786>.
- Friberg, N., Milner, A.M., Svendsen, L.M., Lindegaard, C., Larsen, S.E., 2001. Macroinvertebrate stream communities along regional and physico-chemical gradients in Western Greenland. *Freshw. Biol.* 46, 1753–1764. <https://doi.org/10.1046/j.1365-2427.2001.00857.x>.
- Fuller, R.L., LaFave, C., Anastasi, M., Molina, J., Salcedo, H., Ward, S., 2008. The role of canopy cover on the recovery of periphyton and macroinvertebrate communities after a month-long flood. *Hydrobiologia* 598, 47–57. <https://doi.org/10.1007/s10750-007-9139-5>.
- García-Roger, E.M., Sánchez-Montoya, M.M., Gómez, R., Suárez, M.L., Vidal-Abarca, M.R., Latron, J., Rieradevall, M., Prat, N., 2011. Do seasonal changes in habitat features influence aquatic macroinvertebrate assemblages in perennial versus temporary Mediterranean streams? *Aquat. Sci.* 73 (4), 567–579. <https://doi.org/10.1007/s00027-011-0218-3>.
- García-Roger, E.M., Sánchez-Montoya, M.M., Cid, N., Erba, S., Karaouzas, I., Verkaik, I., Rieradevall, M., Gómez, R., Suárez, M.L., Vidal-Abarca, M.R., Demartini, D., Buffagni, A., Skoulikidis, N., Bonada, N., Prat, N., 2013. Spatial scale effects on taxonomic and biological trait diversity of aquatic macroinvertebrates in Mediterranean intermittent streams. *Fundam. Appl. Limnol.* 183, 89–105. <https://doi.org/10.1127/1863-9135/2013/0429>.
- Gasith, A., Resh, V.H., 1999. Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annu. Rev. Ecol. Syst.* 30, 51–81. <https://doi.org/10.1146/annurev.ecolsys.30.1.51>.
- Giam, X., Chen, W., Schriever, T.A., Van Driesche, R., Muneepeerakul, R., Lytle, D.A., Olden, J.D., 2017. Hydrology drives seasonal variation in dry land stream macroinvertebrate communities. *Aquat. Sci.* 79, 705–717. <https://doi.org/10.1007/s00027-017-0530-7>.
- Gore, J.A., Layzer, J.B., Mead, J., 2001. Macroinvertebrate instream flow studies after 20 years: a role in stream management and restoration. *Regul. Rivers Res. Manag.* 17, 527–542. <https://doi.org/10.1002/rrr.650>.
- Hart, D.D., Finelli, C.M., 1999. Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annu. Rev. Ecol. Syst.* (1), 363–395. <https://doi.org/10.1146/annurev.ecolsys.30.1.363>.
- Heino, J., Muotka, T., Paavola, R., 2003. Determinants of macroinvertebrate diversity in headwater streams: regional and local influences. *J. Anim. Ecol.* 72, 425–434. <https://doi.org/10.1046/j.1365-2656.2003.00711.x>.
- Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., 2016. Species distribution modeling. Documentation for package 'dismo' version 1.0–15. <https://cran.r-project.org/web/packages/dismo/dismo.pdf>, Accessed date: 25 November 2018.
- Juhász, I., 2016. Evaluation of macroinvertebrate data based on autecological information. *Slovak J. Civ. Eng.* 24, 36–44. <https://doi.org/10.1515/sjce-2016-0020>.
- Kalogianni, E., Vourka, A., Karaouzas, I., Vardakas, L., Laschou, S., Skoulikidis, N., 2017. Combined effects of water stress and pollution on macroinvertebrate and fish assemblages in a Mediterranean intermittent river. *Sci. Total Environ.* 603, 639–650. <https://doi.org/10.1016/j.scitotenv.2017.06.078>.
- Karaouzas, I., Smeti, E., Vourka, A., Vardakas, L., Mentzafou, A., Tornés, E., Sergi Sabater, S., Muñoz, I., Skoulikidis, N., Th., Kalogianni, E., 2018. Assessing the ecological effects of water stress and pollution in a temporary river-implications for water management. *Sci. Total Environ.* 618, 1591–1604. <https://doi.org/10.1016/j.scitotenv.2017.09.323>.
- Kooperberg, C., 2018. Package 'logspline'. <https://cran.rproject.org/web/packages/logspline/index.html> (version 2.1.9).
- Lazaridou, M., Ntislidou, C., Karaouzas, I., Skoulikidis, N., 2018. Harmonization of a new assessment method for estimating the ecological quality status of Greek running waters. *Ecol. Indic.* 84, 683–694. <https://doi.org/10.1016/j.ecolind.2017.09.032>.
- Leigh, C., 2013. Dry-season changes in macroinvertebrate assemblages of highly seasonal rivers: responses to low flow, no flow and antecedent hydrology. *Hydrobiologia* 703, 95–112. <https://doi.org/10.1007/s10750-012-1347-y>.
- Leigh, C., Datry, T., 2017. Drying as a primary hydrological determinant of biodiversity in river systems: a broad-scale analysis. *Ecography* 40, 487–499. <https://doi.org/10.1111/ecog.02230>.
- Leunda, P.M., Oscoz, J., Miranda, R., Ariño, A.H., 2009. Longitudinal and seasonal variation of the benthic macroinvertebrate community and biotic indices in an undisturbed Pyrenean river. *Ecol. Indic.* 9, 52–63. <https://doi.org/10.1016/j.ecolind.2008.01.009>.
- Miller, S.W., Wooster, D., Li, J., 2007. Resistance and resilience of macroinvertebrates to irrigation water withdrawals. *Freshw. Biol.* 52, 2494–2510. <https://doi.org/10.1111/j.1365-2427.2007.01850.x>.
- Muñoz, I., 2003. Macroinvertebrate community structure in an intermittent and a permanent Mediterranean streams (NE Spain). *Limnologia* 22, 107–116.
- Poff, N.L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *J. N. Am. Benthol. Soc.* 16, 391–409. <https://doi.org/10.2307/1468026>.
- R Core Team, 2014. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria <https://www.r-project.org/>, Accessed date: 26 September 2018.
- Richards, C., Host, G.E., Arthur, J.W., 1993. Identification of predominant environmental factors structuring stream macroinvertebrate communities within a large agricultural catchment. *Freshw. Biol.* 29, 285–294. <https://doi.org/10.1111/j.1365-2427.1993.tb00764.x>.
- Rocha, L.G., Medeiros, E.S.F., Andrade, H.T.A., 2012. Influence of flow variability on macroinvertebrate assemblages in an intermittent stream of semi-arid Brazil. *J. Arid Environ.* 85, 33–40. <https://doi.org/10.1016/j.jaridenv.2012.04.001>.
- Sánchez-Montoya, M.M., Suárez, M.L., Vidal-Abarca, M.R., 2009. Seasonal and interannual variability of macroinvertebrate reference communities and its influence on bioassessment in different Mediterranean stream types. *Fundam. Appl. Limnol.* 174, 353–367.
- Santos, A.N., Stevenson, R.D., 2011. Comparison of macroinvertebrate diversity and community structure among perennial and non-perennial headwater streams. *Northeast. Nat.* 18, 7–26.
- Skoulikidis, N.T., Karaouzas, I., Gritzalis, K.C., 2009. Identifying key environmental variables structuring benthic fauna for establishing a biotic typology for Greek running waters. *Limnologia* 39, 56–66. <https://doi.org/10.1016/j.limno.2008.01.002>.
- Skoulikidis, N.T., Sabater, S., Datry, T., Morais, M.M., Buffagni, A., Dörflinger, G., Zogaris, S., Sánchez-Montoya, M.M., Bonada, N., Kalogianni, E., Rosado, J., Vardakas, L., De Girolamo, A.M., Tockner, K., 2017. Non-perennial Mediterranean rivers in Europe: status, pressures, and challenges for research and management. *Sci. Total Environ.* 577, 1–18. <https://doi.org/10.1016/j.scitotenv.2016.10.147>.
- Stasinopoulos, M.D., Rigby, R.A., Heller, G.Z., Voudouris, V., De Bastiani, F., 2017. *Flexible regression and smoothing: using GAMLSS* in R. Chapman and Hall/CRC.
- Stitz, L., Fabbro, L., Kinnear, S., 2017. Response of macroinvertebrate communities to seasonal hydrologic changes in three sub-tropical Australian streams. *Environ. Monit. Assess.* 189, 254. <https://doi.org/10.1007/s10661-017-5957-8>.
- Stubbington, R., Greenwood, A.M., Wood, P.J., Armitage, P.D., Gunn, J., Robertson, A.L., 2009. The response of perennial and temporary headwater stream invertebrate communities to hydrological extremes. *Hydrobiologia* 630, 299–312. <https://doi.org/10.1007/s10750-009-9823-8>.
- Stubbington, R., Wood, P.J., Reid, I., Gunn, J., 2011. Benthic and hyporheic invertebrate community responses to seasonal flow recession in a groundwater-dominated stream. *Ecology* 4 (4), 500–511. <https://doi.org/10.1002/eco.168>.

- ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67, 1167–1179. <https://doi.org/10.2307/1938672>.
- ter Braak, C.J.F., 1995. Ordination. In: Jongman, R., ter Braak, C., Van Tongeren, O. (Eds.), *Data Analysis in Community and Landscape Ecology*. Pudoc Wageningen, Netherlands, pp. 91–173.
- Theodoropoulos, C., Vourka, A., Stamou, A., Rutschmann, P., Skoulikidis, N., 2018. Response of freshwater macroinvertebrates to rainfall-induced high flows: a hydroecological approach. *Ecol. Indic.* 73, 432–442. <https://doi.org/10.1016/j.ecolind.2016.10.011>.
- Thompson, R.M., Townsend, C.R., 1999. The effect of seasonal variation on the community structure and food-web attributes of two streams: implications for food-web science. *Oikos* 87, 75–88. <https://doi.org/10.2307/3546998>.
- Tonkin, J.D., Bogan, M.T., Bonada, N., Rios-Touma, B., Lytle, D.A., 2017. Seasonality and predictability shape temporal species diversity. *Ecology* 98 (5), 1201–1216.
- van de Bund, W., 2009. Water framework directive intercalibration technical report. Part 1: Rivers. JRC Scientific and Technical Reports, EUR 23838 EN/1, p. 136 <https://doi.org/10.2788/23384>.
- van Vliet, M.T., Franssen, W.H., Yearsley, J.R., Ludwig, F., Haddeland, I., Lettenmaier, D.P., Kabat, P., 2013. Global river discharge and water temperature under climate change. *Glob. Environ. Chang.* 23 (2), 450–464.
- Ward, J.V., Tockner, K., Schiemer, F., 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. *River Res. Appl.* 15, 125–139. [https://doi.org/10.1002/\(SICI\)1099-1646\(199901/06\)15:1/3<125::AID-RRR523>3.0.CO;2-E](https://doi.org/10.1002/(SICI)1099-1646(199901/06)15:1/3<125::AID-RRR523>3.0.CO;2-E).
- Wood, P.J., Armitage, P.D., 2004. The response of the macroinvertebrate community to low-flow variability and supra-seasonal drought within a groundwater dominated stream. *Arch. Hydrobiol.* 161, 1–20. <https://doi.org/10.1127/0003-9136/2004/0161-0001>.
- Wooster, D.E., DeBano, S.J., 2018. The importance of scale in understanding the effect of stream intermittence on aquatic macroinvertebrate diversity. *River Res. Appl.*, 1–11 <https://doi.org/10.1002/rra.3352>.
- Wright, J.F., 2000. An introduction to RIVPACS. In: Wright, J.F., Sutcliffe, D.W., Furse, M.T. (Eds.), *Assessing the Biological Quality of Fresh Waters: RIVPACS and Other Techniques*. Freshwater Biological Association, Ambleside, pp. 1–24.
- Zhang, D., 2018. R-squared and related measures. Documentation for the R package 'rsq'. Version 1.1. <https://cran.r-project.org/web/packages/rsq/rsq.pdf>, Accessed date: 17 January 2019.